THE CHEILOSTOMATOUS POLYZOA *NEOEUTHYRIS WOOSTERI* (MacGILLIVRAY) AND *REGINELLA DOLIARIS* (MAPLESTONE)

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CONTENTS

1. ABSTRACT

Neoeuthyris woosteri (MacG.), unlike the other undoubted members of the Euthyrisellidae (in which ovicells are vestigial or absent), has well developed ovicells. *Urceolipora*, removed from the family by Harmer, has ovicells with some likeness to those of *Neoeuthyris*.

There is evidence of a tendency to reduction of the ovicells of the Cheilostomata, but our knowledge of the factors concerned is still insufficient to frame an explanation.

Metracolposa Canu & Bassler is a synonym of *Reginella* Jullien. *Metracolposa mucronata* Canu & Bassler falls within the range of variation of *Reginella furcata* (Hincks) of which it is thus a synonym.

Cellepora doliaris Maplestone is a member of the Cribrilinidae. Its zooecia have much in common with those of *Reginella*, to which it is tentatively referred. The cribriform frontal shield of its erect zooecia faces the periphery of the low conical colony which is built with a profusion of kenozooecia and avicularia, apparently budded from the septula of the zooecia.

Though belonging to a different major systematic group, the zoarium of *R. doliaris* shows parallel features to that of *Conescharellina* and helps to elucidate the arrangement of the zooecia in the Conescharellinidae.

2. *NEOEUTHYRIS* Bretnall

Neoeuthyris Bretnall, 1921 : 157 ; Hastings, 1960 : 244, 245 ; Opinion 617, 1961 : 363.

Type-species : *Euthyris woosteri* MacGillivray, by monotypy.

The status of the generic name *Neoeuthyris* Bretnall, and of the name of its type-species, was established by Opinion 617 of the International Commission on Zoological Nomenclature. It remains to discuss the material of *N. woosteri* in the British Museum.

2a. *Neoeuthyris woosteri* (MacGillivray)

Text-figs. 1, 2

Euthyris woosteri MacGillivray, 1891 : 77, pl. 9, figs. 2, 2a.

Neoeuthyris woosteri Bretnall, 1921 : 157, text-fig. 1 ; Hastings, 1960 : 244 ; Opinion 617, 1961 : 363.

Distribution : Cooktown, Queensland, on an alga (MacGillivray ; Bretnall) ; Western Australia, on *Metamastophora plana* (Gray ; 1938.8.10.1) ; Fremantle, Western Australia, on part of one of four specimens of *Metamastophora plana*, Harvey's Australian Algae, No. 442 (1948.3.12.1, transferred from Department of Botany).

HOLOTYPE : Cooktown, Queensland, divided between National Museum of Victoria, Melbourne, Victoria (MacGillivray's specimen), and Australian Museum, Sydney, N.S.W. (the rest of the specimen from which MacGillivray's lobe was taken, U.875. Being part of the same specimen this, too, is holotype, not a paratype, c.f. Bretnall, 1921 : 159).

REMARKS : As already noted (Hastings, 1960 : 245), 1938.8.10.1 is the type-material of *Lichenella brentii* Gray (1858), and the algal portion, there chosen as lectotype of Gray's species, is now in the Botanical Department of the British Museum (Nat. Hist.). No intact Polyzoa remain on this lectotype material, though some basal and lateral walls are to be seen. The part including the Polyzoan has been retained in the Zoological Department under the original number.

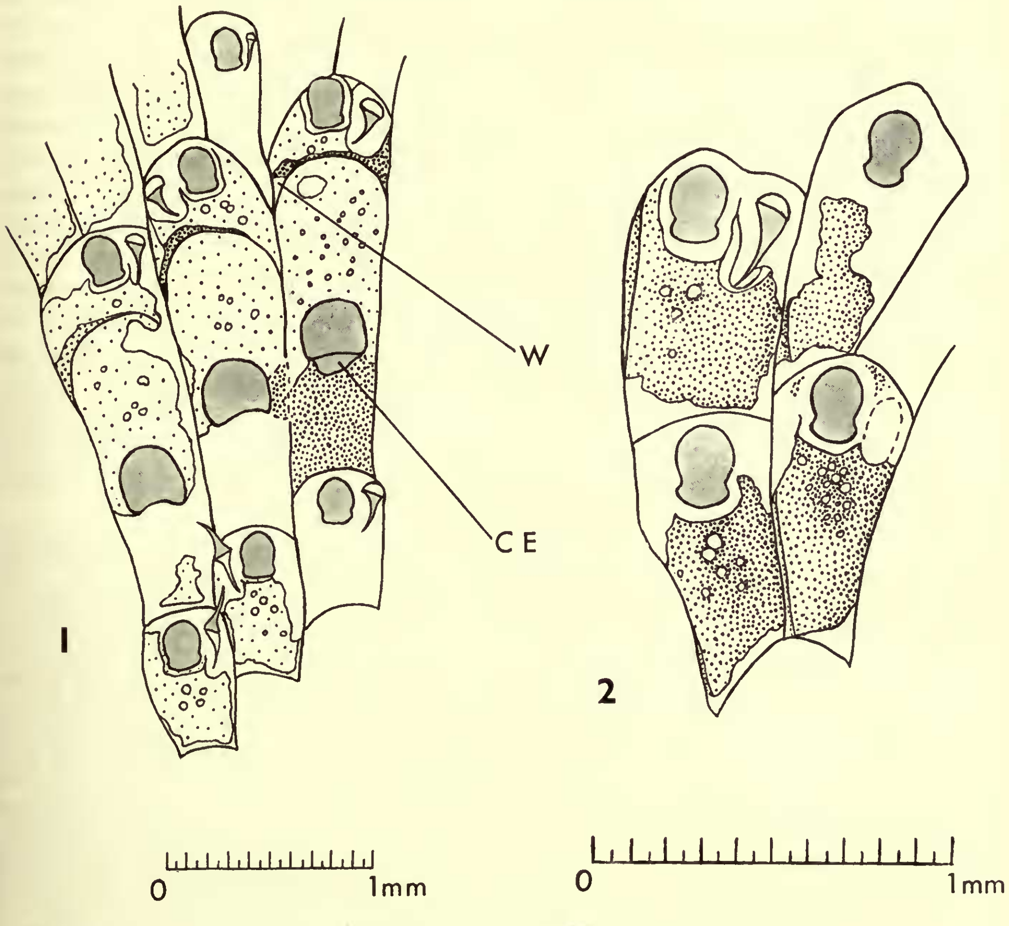
The known colonies of *N. woosteri* all encrust algae and cause a wrinkling of the surface of the encrusted fronds. MacGillivray described the species from a single lobe from a colony whose form was unknown. Bretnall examined the whole, small specimen from which MacGillivray's lobe was taken (Australian Museum, U.875), and established the algal nature of the basal layer. The basal surface, as described by MacGillivray, is like the basal algal layer in Gray's specimen. Miss Elizabeth Pope has very kindly examined the specimen in the Australian Museum, in which one fragment is mounted to show the alga, and she has confirmed the presence of ridges similar to those in Gray's specimen.

No. 442 of Harvey's Australian Algae in the British Museum consists of four specimens of *Metamastophora plana*, one of which bears extensive growths of *Neoeuthyris*. The contrast between the ridged surface of the parts of the fronds bearing the polyzoan, or remains of it, and the smoothness of the colonized parts is striking. It is also interesting to find that a photograph of a specimen which, Mr. Ross tells me, is presumably part of the type-gathering of *Metamastophora plana* shows exactly similar ridges on the fronds (Foslie, 1929, pl. 25, fig. 5).

The colonies of *N. woosteri* are very fragile, being delicately calcified and covered with a thin epitheca which readily breaks away. My material is all old (Gray's specimen has been in the Museum for over a century) and has been dried and preserved between paper as herbarium material. The specimens are therefore considerably damaged. Further, the epitheca may be obscured by a thin growth of a calcareous alga. Fortunately, enough remains intact to show the essential features of the anatomy and the beauty of the species. In fact the damage is sometimes helpful, for zooecia are to be found in which the loss of the epitheca exposes the underlying calcareous parts, others in which the fracture of the calcareous wall exposes the floor of the compensation sac, and others again in which the compensation sac has also been destroyed exposing the interior of the zooecium.

As in *Euthyrisella obtecta* (Hincks), the epitheca is stretched above the depressed, calcareous, frontal wall. It is attached to the raised rim (marginal walls) of the zooecium, the raised rim of the orifice, and the papillae on the frontal wall (Text-fig. 2).

I have not examined the type-material of *Neoeuthyris woosteri* myself, but the species is readily recognizable from the accounts given by MacGillivray and Bretnall, both based on the type-material. The British Museum specimens agree very closely with these accounts, except that they have two types of orifice (Text-fig. 1) resembling the 'A' and 'B' orifices of the other two species of *Euthyris*



FIGS. 1 AND 2. *Neoeuthyris woosteri* (MacGillivray), 1948.3.12.1.

1. Part of the colony, showing three ovicells. Epitheca white, underlying calcareous parts (exposed where epitheca has been lost) lightly stippled, fractures darkly stippled, opercula and mandibles mechanically stippled. *CE*, chitinized proximal extension of operculum; *W*, bit of frontal wall by ovicell in situ. 2. Four non-fertile zooecia. Epitheca white, underlying calcareous parts (exposed where epitheca has been lost) shaded, opercula and mandible mechanically stippled. On the left side of each zooecium part of the raised rim and the depressed frontal wall of the zooecium can be seen. One complete avicularium and one rudiment (outlined with broken line).

(s. lat.), namely, *Euthyrisella obtecta* (Hincks, 1882a : 165, pl. 7, fig. 3) and *Pleurotoichus clathrata* (Harmer, 1902 : 266, pl. 16, figs. 20, 21). As 'B' zooecia are rather rare in the British Museum material of *Neoeuthyris woosteri*[1] their complete absence from the small pieces of type-material is not surprising, and I am satisfied that the specimens I have examined belong to MacGillivray's species.

The difference between the two kinds of orifice is more marked than in *Euthyrisella obtecta*, as the few 'B' orifices of *Neoeuthyris woosteri* that I have seen are slightly wider and the 'A' orifices are markedly narrower than those of *E. obtecta*. The 'B' orifices of the two species are similar in shape, but the 'A' orifices of *E. woosteri* are somewhat narrowed towards the proximal end and have more pronounced lateral indentations. The latter are well figured by MacGillivray.

Harmer (1902 : 270) remarked that the separate proximal wall of the zooecium in *Pleurotoichus clathratus* "suggests that the 'B' zooecia possess a vestigial ovicell," and his figure (pl. 16, fig. 21) justifies this interpretation. It is therefore interesting to find that the 'B' zooecia of *Neoeuthyris woosteri* bear exceptionally large, fully developed ovicells (Text-fig. 1).

In *Euthyrisella obtecta*, on the other hand, the 'B' zooecia show no trace even of a vestigial ovicell. I have examined the beautiful, stained preparation figured by Harmer (1902, pl. 16, figs. 33, 37, Haddon Coll., Torres Straits, 1916.8.23.115) without obtaining any further evidence as to whether the 'B' zooecia are fertile.

Thus in three species referred to the Euthyrisellidae, all of which have dimorphic orifices, we find *Euthyrisella obtecta* with no ovicells, *Pleurotoichus clathratus* with traces of ovicells, and *Neoeuthyris woosteri* with exceptionally large ovicells, a matter which I discuss further below.

The ovicells of *N. woosteri* are immersed in the zooecium distal to the fertile zooecium. The former are longer and broader than the ordinary zooecia, and the ovicells occupy three-fourths of their length and their whole breadth (Text-fig. 1). In each instance this large zooecium gives rise to two distal zooecia. The ovicell bears a few calcareous papillae like those on the frontal wall. Its lip turns upward to the level of the rim of the zooecial orifice and it is closed by the operculum of the fertile zooecium. The calcareous frontal wall of the zooecium containing the ovicell descends more steeply from the orifice than that of the ordinary zooecia, and ends abruptly against the distal end of the ovicell. Unfortunately, this wall is in every instance more or less broken where it meets the ovicell. One small piece has, however, remained in its proper position in the right-hand figured zooecium (Text-fig. 1, W). The epitheca of the zooecia containing the ovicells is much damaged, but sufficient remains on the left-hand ovicell in Text-fig. 1 to show that it extended over the frontal surface of the zooecium at the usual level without moulding itself to the contours of the underlying descending wall and ovicell.

The ovicellular (B) operculum has a chitinized, proximal extension (Text-fig. 1, CE) behind the proximal sclerite. The figured example is incomplete : when undamaged this extension is wider and symmetrical.

[1]There are three in 1948.3.12.1 (see fig. 1) and five in 1938.8.10.1.

Bretnall (1921 : 159) suggested that the specimen of *Euthyris* mentioned by Levinsen (1909 : 273, obtained from Mr. C. N. Peal) may have belonged to *Neoeuthyris woosteri*. I have been unable to trace Mr. Peal's specimen.

N. woosteri is not included in Livingstone's check-list of Queensland Polyzoa (1927).

Generic Position : All the three species discussed above were referred at first to *Euthyris* Hincks (1882a : 164, type-species *E. obtecta*). This name is preoccupied by *Euthyris* Quenstedt (1869 : 442, 718), a genus of Brachiopoda. Bassler (1936 : 161) introduced *Euthyrisella* to replace it.

MacGillivray regarded his species as congeneric with *Euthyrisella obtecta*. Harmer (1902 : 268) doubted whether they were congeneric (there is no evidence that he had seen a specimen of MacGillivray's species) ; and Bretnall, after examining MacGillivray's type-material, considered that it was generically distinct, and made *Euthyris woosteri* the type of a new genus *Neoeuthyris*. He based this opinion chiefly on the absence of dimorphism of the orifices, a distinction which we now know to be invalid, and on the presence of avicularia.

Neoeuthyris woosteri resembles *Euthyrisella obtecta* in the relation of the epitheca to the underlying, calcareous frontal wall, in the presence of a few calcareous papillae on this frontal wall proximally to the orifice (cf. Harmer, 1902, pl. 16, fig. 32), and in possessing orifices of two kinds. I have not seen pores, except for one or two small ones which may be present in the wall of the avicularian chamber near its junction with the frontal wall. *Neoeuthyris woosteri* differs from *Euthyrisella obtecta* in the presence of avicularia (well figured by MacGillivray), in the presence of ovicells, and in the colony which is encrusting and without the basal papillae and raised basal epitheca found in *E. obtecta*.

These differences together may justify the generic separation, but individually none of them is of great significance. The presence or absence of avicularia, and the form of the colony are generally recognized as frequently not of generic significance, and I have given evidence below that the presence or absence of ovicells may also be unimportant generically. On the other hand, the close similarity of the frontal wall to that of *Euthyrisella obtecta* with its papillae and raised epitheca, and the general resemblance of the 'A' and 'B' zooecia are important points of resemblance. If *Neoeuthyris woosteri* and *Euthyrisella obtecta* are congeneric, the name *Euthyrisella* becomes a synonym of the earlier *Neoeuthyris*.

Bretnall quoted the definition of the Euthyridae[1] given by Levinsen (1909 : 269), who included *Urceolipora* MacGillivray in the family and therefore mentioned the ovicells of that genus in the definition. Levinsen (p. 271) described these ovicells as " of a most peculiar structure, being endozooecial and at the same time having their endooecium situated frontally to the cryptocyst of the zooecium, which is much excavated to receive its arched basal surface ". His description and figure

[1]Replaced by Euthyrisellidae by Bassler (1953 : G226). If *Euthyrisella* were regarded as a synonym of *Neoeuthyris* no further change of family name would be necessary according to Article 40, Rules of Zoological Nomenclature, 1961 : 41.

appear to be accurate,[1] but his interpretation of the structures seen is puzzling.

The relationship of the ovicell of *Neoeuthyris* to the flat frontal membrane and descending calcareous wall of the distal zooecium suggests comparison with *Urceolipora*, but it is possible that the calcareous wall does not extend beneath the ovicell. The point is important in determining whether *Urceolipora* should be separated from the Euthyrisellidae (see Harmer, 1957 : 874), but fresh material of *Neoeuthyris* is needed before it can be settled.

3. REDUCED AND VESTIGIAL OVICELLS

I hope to discuss some of the problems concerning the ovicells of the Cheilostomata in another paper, but the marked differences in the brooding arrangements among the Euthyrisellidae, noted above, need some comment here.

There is increasing evidence that, although the structure of the ovicells, when present, may be of considerable taxonomic significance, their presence or absence is sometimes not even a generic character. Levinsen (1909 : 72) commented on this, but my attention was particularly drawn to it by the comments of Harmer (1926), who recorded a number of pairs of species in which one member of the pair has a well developed ovicell, and the other, while very similar in other respects, has a shallow ovicell incapable of accommodating the embryo ; or no ovicell at all, the embryo then occupying a sac in the body-cavity. Examples of such pairs are :— *Carbasea linguiformis* and *C. pedunculata* (pp. 249, 250), *Retiflustra cornea* and *R. schönaui* (p. 253), *Farciminellum alice* and *F. atlanticum* (p. 405), *Bugula johnstonae* and *B. longicauda* (p. 451), and, among the Ascophora, *Tetraplaria ventricosa* (Haswell) and *T. immersa* (Haswell), see Harmer (1957 : 1053, 1055).

I have examined several similar instances, notably *Umbonula ovicellata* and *U. littoralis* (see Hastings, 1944 : 273, 274), *Crassimarginatella exilimargo*, *C. marginalis* and *C. spatulifera* (see Hastings, 1945 : 78, 84), *Carbasea papyrea* and *C. carbasea* (see Norman, 1903 : 582. *C. solanderi* Norman = *C. carbasea*).

Cornucopina polymorpha and *C. infundibulata* (see Hastings, 1943 : 397, 399) are of especial interest because the well developed ovicells of the one species and the shallow ones of the other are both borne on special, small zooecia which are not found in other species of the genus, and there are thus particularly strong reasons for thinking that the two species are very closely related.

Harmer (1926 : 411 *et seq.*) noted less closely paired examples in *Beania* ; while *Himantozoum*[2] (see Hastings, 1943 : 423) shows a gradation from the species with fully formed ovicells to species in which the fertile zooecia show little or no trace of an ovicell. The gradation of the ovicells of *Camptoplites* (see Hastings, 1943 : 436, etc.) and *Bugula* (Hastings, MS) are interesting in this connection. See Addendum.

The members, hitherto known, of a certain group of species of *Bugula* all have distinctive, globular, obliquely placed ovicells. Ryland (1963 : 23) has recently

[1]Harmer (1957, text-fig. 94, p. 874) gave a figure of *U. nana* which appears to differ from Levinsen's in the relationship of the ovicell to the calcareous frontal wall (Levinsen's cryptocyst). The figure is, however, diagrammatic and simplified, and the specimen on which it was based (Cambridge Museum, reg. May 13, 1899) agrees with Levinsen's figure.

[2]Silén (1951 : 63) made the illuminating suggestion that this genus appears to be more nearly related to the Farciminariidae than to the Bicellariellidae with which it has hitherto been placed.

described a new species, *B. gautieri*, agreeing with this group in other respects, but having extremely vestigial, symmetrically placed ovicells, and an internal ovisac.

In the examples so far mentioned the differences in the ovicells are specific. Some pieces of *Crassimarginatella spatulifera* Harmer (1926 : 223), collected off Formosa (119° 35′ E, 23° 32′ N) by Prof. T. Y. H. Ma (1961.2.20.2) are of particular interest in showing a range of variation in the development of the ovicells within the one sample of one species, and, indeed, within the individual fragments. Some of the ovicells are fairly prominent, rounded and immediately recognizable as ovicells, though shallow. At the other extreme, the slight modification of the distal end of the zooecium, which is all there is to represent the ovicell, deserves to be called vestigial (c.f. Harmer, 1926, pl. 14, fig. 2).

Among the members of the Euthyrisellidae discussed in this paper the instance of *Euthyrisella obtecta* and *Neoeuthyris woosteri* (which are so much alike in many ways, and may be congeneric) is particularly striking.

It will be noticed that the examples quoted include some pairs in which the well-developed ovicell is hyperstomial, and others where it is endozooecial. The small ovicells are usually called reduced or vestigial. The latter term should perhaps be reserved for the extreme cases where the external structure would hardly be recognized as an ovicell were it not for the evidence of the internal ovisac, see, for example, *Bugula longicauda* Harmer (1926 : 450, pl. 30, fig. 15). In some instances Harmer has put forward the view that an evolutionary reduction is responsible (e.g. Harmer, 1926 : 405). It is certainly hard to imagine that the fully developed ovicells of the various genera could have been evolved independently and reached their similarity by convergence.

It is difficult to find any explanation of this tendency to reduction of the ovicells. In considering the pairs of species, I noted the depths at which the various pairs have been found, but no constant relationship was to be observed ; nor is any general geographical or climatic correlation discernible. The examples mentioned are from localities throughout the world and with very diverse climates.

In the European pairs mentioned (*Umbonula ovicellata* and *U. littoralis*, and *Carbasea papyrea* and *C. carbasea*) the species with the internal ovisacs has a more northerly range than the one with ovicells ; but there are *Umbonula* species farther north which reverse this relationship.[1]

Carbasea carbasea and *C. papyrea*, on the other hand, appear to be an example of a more general north and south (arctic or boreal and mediterranean) pairing, not specially associated with brooding arrangements, nor peculiar to the Polyzoa. Nordgaard (1918 : 92, 95), discussing the distribution of the arctic and Norwegian Polyzoa, listed several such instances among which the northern *Porella compressa* (Sowerby) and the mediterranean *P. cervicornis* (Pallas) are a well-known pair. Nordgaard wrote (p. 95) that he had come to the conclusion that there is a dualism in the species of northern animals. " To a southern form there is often a nearly related northern, to a tertiary species there may be commonly found a quaternary

[1] *U. ovicellata* (Mediterranean to S.W. Britain) : ovicells. *U. littoralis* (English Channel to Norway and Denmark) : no ovicells. *U. arctica* (Boreal and Arctic) : no ovicells. *U. patens* (Arctic) : ovicells. (See Hastings, 1944 : 277, 282, and Osburn, 1952 : 298, 299).

pendant." In a valuable zoographical discussion, he tried to relate this dualism to the effect of the cooling northern climate on a warm-water (mediterranean-type) Tertiary fauna. Unfortunately the palaeontological data are not yet adequate, though the revision of the Pliocene Polyzoa of the Low Countries by Lagaaij (1952) provides much useful information.

Borg (1933 : 141) also noted north and south pairing of Polyzoan forms, but within the boreal and arctic zones. He stated that not a few species designated as boreal or arctic-boreal are vicariously replaced in the true Arctic by more or less distinct varieties or by species. He listed 21 examples. Again there is no correlation with brooding arrangements.

Much more knowledge of the ovicells themselves, and also of these more general examples of pairs of species, is needed before an explanation of the observed tendency to reduction of polyzoan ovicells can be attempted. In the meantime one can only draw attention to the problem.

4. *REGINELLA* Jullien

Reginella Jullien, 1886 : 605 ; Canu, 1900 : 446 (as a subgenus of *Cribrilina*) ; Canu & Bassler, 1920 : 283 ; 1929 : 243 (English translation of Jullien's definition) ; Osburn, 1950 : 178 ; Brown, 1958 : 52.

Metracolposa Canu & Bassler, 1917 : 34 ; 1920 : 283, 304 ; Osburn, 1950 : 179.

Type-species of *Reginella : Cribrilina furcata* Hincks, 1882b : 250 ; 1882c : 470, pl. 20, fig. 5. Figure reproduced in Canu, 1900 : 446, text-fig. 61, and Canu & Bassler, 1920 : 282, text-fig. 18N. Recent, Queen Charlotte Islands.

Type-species of *Metracolposa : Metracolposa robusta* Canu & Bassler, 1917 : 35, pl. 3, fig. 6. Figure reproduced, 1920, pl. 43, fig. 3. Eocene, North Carolina.

Jullien apparently introduced his genus on the basis of Hincks's figure. This shows the lacunae (intercostal spaces) occupying polygonal areas, and Jullien accordingly included this character in his generic definition, which has been translated and quoted. Hincks does not mention these areas, and they are not shown in Osburn's figures. In the British Museum specimen (1886.3.6.17–18) some of the intercostal connexions are markedly convex, like the costae. The lacunae are then at the bottom of a series of regular hollows which, in certain lights, appear to be outlined ; but this can readily be shown to be no more than an effect of light and shade.

Osburn redescribed *R. furcata*, and referred certain other species to the genus. He suggested that *Metracolposa* might be synonymous with *Reginella*, from which it differs in its escharan colony and in possessing avicularia. I think he was right. I have not seen a specimen of the type-species of *Metracolposa*, but in view of the very close similarity of its zooecia and ovicells to those of *Reginella*, I cannot regard its escharan colony and the presence of avicularia as distinguishing it generically. Interzooecial communication by means of septula has been recorded for the type-species of both genera (Osburn, 1950 : 179 ; Canu & Bassler, 1920, pl. 43, fig. 6). The zooecial operculum closes the ovicell in *R. furcata* and Canu & Bassler deduced (from the hard parts of the fossil type-species) that it also did so in *Metracolposa*.

Waters (1904 : 42) noted agreement between his antarctic species, *Cribrilina projecta*, and *Reginella*. Brown (1958 : 53) considered that *C. projecta* and certain other species discussed by him " are evidently congeneric with *Reginella furcata* ". My own study (unpublished) of the specimens of *Cribrilina projecta* in the collections of the Discovery Investigations, as well as Waters's type-material, indicates that this species is not congeneric with *Reginella furcata*.

4a. ***Reginella furcata*** (Hincks)

Cribrilina furcata Hincks, 1882b : 250 ; 1882c : 470, pl. 20, fig. 5 ; O'Donoghue, 1923 : 172 ; Waters, 1924 : 609, pl. 19, fig. 5 (ancestrula).
Reginella furcata Jullien, 1886 : 605 ; O'Donoghue, 1925 : 101 ; 1926 : 98 ; Osburn, 1950 : 179, pl. 28, fig. 3 ; Androsova [1960?] : 44, 59, pl. 1, fig. 4
Metracolposa mucronata Canu & Bassler, 1923 : 92, pl. 35, fig. 4.
Reginella mucronata Osburn, 1950 : 180, pl. 28, fig. 4, pl. 29, fig. 3 ; Soule & Duff, 1957 : 104 ; Soule, 1959 : 46 ; Hertlein & Grant, 1960 : 86 (record only).

Distribution : Recent. Pacific coast of America from Queen Charlotte Islands to Lower California (see Osburn and Soule) ; Yellow Sea (Androsova). Fossil. Pleistocene and Pliocene, California (see Soule & Duff and Hertlein & Grant).

Material examined : 1886.3.6.17, 18, Queen Charlotte Is., presented by the Geol. & Nat. Hist. Survey of Canada and determined by Hincks. 1921.11.17.12, Departure Bay, Vancouver Is., B.C., presented and determined by Dr. C. H. O'Donoghue.

Remarks : If *Metracolposa* were retained as a distinct genus, *M. mucronata* Canu & Bassler, which is not known to have avicularia and is encrusting, would still have to be placed in *Reginella*, where Osburn placed it. He recognized it as closely akin to *R. furcata*. According to his key and description, they agree in the general characters of the frontal shield, in the ovicell and ancestrula, in their dimensions, and in the absence of avicularia ; they differ in the presence of oral spines in *R. furcata* (absent in *R. mucronata*), in the proximal lip of the aperture (apertural bar in key, p. 179) which is described (p. 181) as " stronger and more or less bimucronate " in *R. mucronata*, and in the more variable number of lumen pores in *R. furcata* (2–4 oval pores compared with 2 small round pores in *R. mucronata*).

I think, however, that these distinctions do not hold. Osburn has himself remarked (p. 181) that the spines are often " wanting " in *R. furcata ;* and Hincks described and figured " a peristome rising in front to a central mucro ". The Queen Charlotte Island specimen of *R. furcata* in the British Museum shows considerable variation in the apertural bar. It may be unthickened or thickened, non-mucronate or with a mucro of variable form, in one instance slightly bifid. O'Donoghue's specimen has more of the zooecia with a thickened, mucronate bar, and the mucro is often bifid (" bimucronate ") as in *R. mucronata*, but the specimen has oral spines. Osburn figured the costae as completely transverse in *R. furcata*, but radiating proximally in *R. mucronata*. In this, however, the British Museum material of *R. furcata* and Canu & Bassler's figure of *R. mucronata* both show variation.

The zooecial operculum closes the ovicell in *R. furcata*, but according to Canu &

Bassler's description it did not do so in *R. mucronata*. There seems, however, to be nothing to indicate such a difference between *R. mucronata* and *R. robusta* (see above), so I think that their statement must have been a slip, and that both of these fossil species probably agreed with *R. furcata* in this respect. Osburn did not mention this character in his descriptions of *R. furcata* and of the recent material which he referred to *R. mucronata*.

The evidence thus indicates that *R. mucronata* is a synonym of *R. furcata*.[1]

One of O'Donoghue's colonies of *R. furcata* (1921.11.17.12) has an ancestrula, and shows, in comparison with Waters's figure of a specimen from British Columbia, that there is some variation in the details of the early stages of the colony. O'Donoghue's ancestrula has 13 marginal spines (Waters showed 10), and it has given rise to only 2 zooecia distally. It has 2 small distal spines (one represented by its base only), 5 moderately erect lateral spines (or remains of spines) on each side, and the base of a median, proximal spine. The first two zooecia have each formed a pair of distal buds, and, by continued budding, a fan-shaped colony has been produced.

The pointed structures in, or over, the orifice in the figure given by Androsova (1960? pl. 1, fig. 4) are presumably the forked spines, c.f. Osburn (1950, pl. 28, fig. 3).

4b. ***Reginella doliaris*** (Maplestone)

Pl. 1, figs. 1–3, pls. 2, 3

Cellepora doliaris Maplestone, 1909 : 272, pl. 77, figs. 10 a, b.
Reginella doliaris Brown, 1958 : 53.

MATERIAL EXAMINED : One dry colony, marked " co-type," 1909.11.12.14, 22 miles E. of Port Jackson, c. 80 fms. (the only known locality), presented by the University of Sydney, N.S.W.

DESCRIPTION : *Zoarium* (pl. 1, figs. 1–3) apparently free, low conical, with concave, oval base with axes *c.* 3·5 and 3 mm., the zooecial orifices on the convex surface, their proximal ends at the concave surface, the thickness of the zoarium at the edge being the length of the zooecia (pl. 1, fig. 3, pl. 3, figs. 1, 2, 5). Small chambers (interpreted as kenozooecia), with finely granular walls, occupying the interstices between the zooecia laterally and on the convex surface of the colony, and filling the concavity (pl. 2, fig. 1, pl. 3, figs. 1–5). Avicularia frequent on both surfaces.

Zooecia erect, with cribrimorph frontal shield, this frontal wall facing the periphery of the zoarium, the proximal end of the zooecium rounded without distinction of proximal from lateral walls (pl. 3, figs. 4, 5), orifice in a plane oblique to that of frontal shield.

Frontal shield (pericyst[2]) *c.* 0·1 mm. × 0·5 mm. with 9–13 regular costae with an

[1] I have not considered the validity of the other species recognized by Osburn.

[2] *Frontal shield*, term introduced by Harmer, 1902 : 282 footnote.
Pericyst, synonymous term, introduced by Canu & Bassler, 1929 : 115 footnote.
For definitions of these and other terms see Bassler's valuable glossary (1953 : G7–G16).

even series of small lacunae between them (pl. 3, fig. 1), costae transverse except proximally where they radiate, the apertural bar stout, in the best preserved zooecia rising to a short blunt median point (pl. 3, fig. 3), elsewhere more or less worn, appearing irregular, occasionally denticulate, or smooth.

Orifice nearly circular with very slight constrictions marking off a deep anter from a shallow poster.

Oral spines four, erect, broad, flattened, slightly bifid (pl. 2, fig. 2) ; distal pair fused to form a distal plate,[1] the suture, visible as a groove on the outer surface[2] of the plate, running from a small pit at the base, this little hollow visible when rest of suture obliterated ; outer spines beside orifice, somewhat curved, taller than the plate and touching it laterally ; spines and plate partially or completely worn away in older zooecia.

Operculum presumably delicate, not articulating with the frontal shield (shrivelled remains sometimes visible within the orifice at a deeper level than the apertural bar).

Septula in a regular row just below the bases of the costae (pl. 3, fig. 4), extending round proximal end of zooecium, generally hidden by kenozooecia.

Kenozooecia developed as a linear series along lateral walls and round proximal end of each zooecium (pl. 3, figs. 1, 2), apparently originating from the septula.

Avicularia commonly (but not on every zooecium) replacing a distal lateral kenozooecium on one or both sides of a zooecium, and also the median proximal kenozooecium (pl. 3, fig. 1). As more zooecia develop, these avicularia come to lie on the two surfaces of the colony, those on the convex surface (pl. 2, fig. 1) lying beside the orifice at a little distance from it (this follows from their development as distal members of the lateral series of kenozooecia), the proximal ones mingling with the kenozooecia filling the concavity (pl. 1, fig. 3). Avicularian chambers prominent, rounded, somewhat tapering proximally to give " cornucopia-shape " described by Maplestone. Beak strong and very bluntly pointed. Mandible a rounded, nearly equilateral triangle, articulated to condyles.

Ovicells not found.

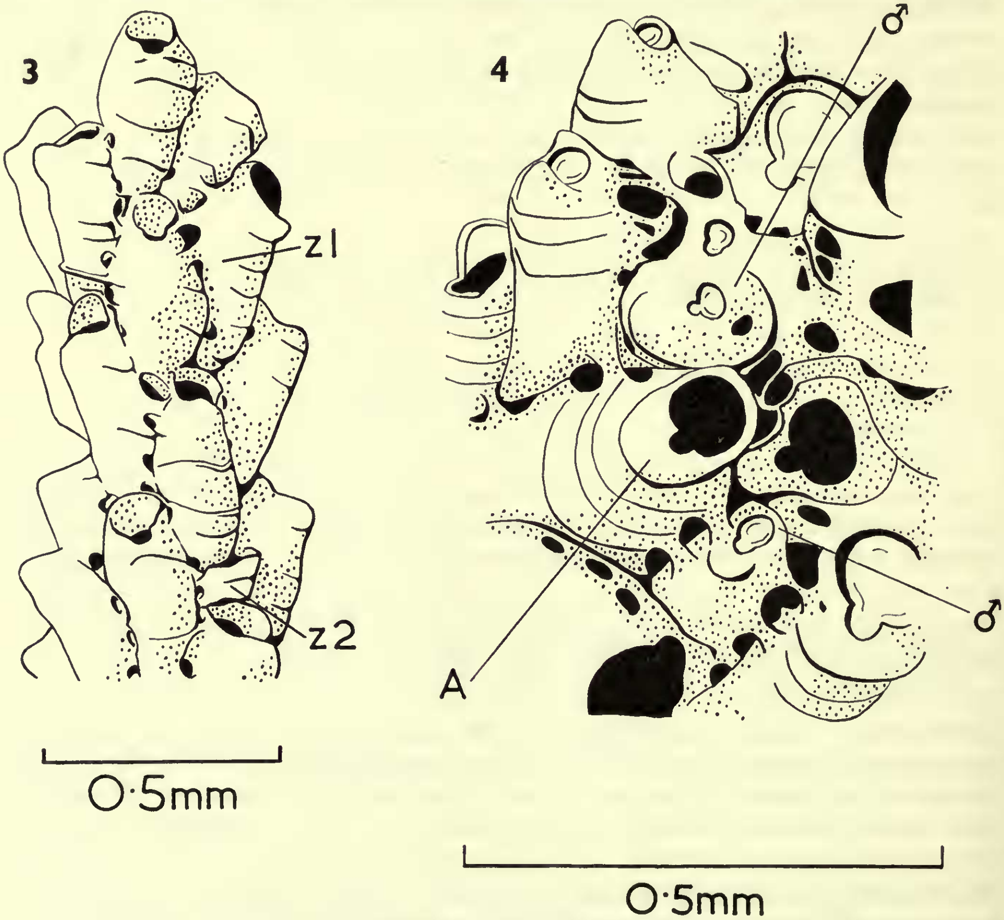
REMARKS : In the younger parts of the colony the zooecia are immersed so that little more than the border of the orifice (apertural bar, spines and distal plate) projects at the surface of the colony, but a few zooecia (in particular three at the apex) project further showing part of the cribriform wall (pl. 1, fig. 2, pl. 2, fig. 1). One of the apical ones has this wall exposed for about half its length. These apical zooecia show the extremely abraded condition in which the spines and distal plate are worn right down to their base, and the apertural bar is also worn smooth.

There is only one point where there is any trace of an incomplete zooecium. It takes the form of a low, curved, proximal wall applied to the cribriform surfaces of two neighbouring zooecia (pl. 3, fig. 5). These zooecia overlie each other in such a way that the lateral kenozooecia of one zooecium are applied to the frontal wall

[1]The term *distal plate* was used by Lang (1916 : 82 ; 1921 : 46–47) for similar structures in Cretaceous Cribrimorph Polyzoa.
[2]*Outer surface*, i.e. the surface away from the orifice.

of the one partially covered by it (pl. 3, figs. 1, 2, 5). The zooecial rudiment lies mostly on the underlying zooecium, and appears to originate from one of the more proximal members of the lateral series of kenozooecia of the upper zooecium. The arrangement of the zooecia in the colony indicates that the position of this bud represents the usual point of origin of the new zooecia.

The relation to each other of the various kinds of zooecia in the colony of *Hippothoa hyalina* (s. lat.) is sometimes strictly comparable to that of the zooecia of *Reginella doliaris*, as just described. For example, Marcus (1938, pl. 20, fig. 56) showed the



FIGS. 3 AND 4. *Hippothoa* sp. False Bay, South Africa, 1963.1.12.1.

3. Recumbent zooecia showing chambers along the interzooecial grooves, and the beginning of the growth of superficial layers. *z*1, complete zooecium overlapping frontal surface of two neighbouring zooecia ; *z*2, proximal part of incomplete zooecium applied to the frontal surface of another zooecium. 4. Erect, jumbled growth showing male zooecia applied to frontal surface of asexual zooecia, and also the converse relationship. ♂, male zooecium applied to asexual zooecium ; *A*, asexual zooecium overlapping two male zooecia and another asexual zooecium. Drawings by Miss P. L. Cook.

sexual zooecia arising in the interzooecial grooves and applied by their basal surface to the frontal surface of the neighbouring asexual zooecia. The asexual zooecia may also be applied to the frontal surface of their neighbours in the same way. In a specimen of *Hippothoa* sp. from South Africa (False Bay, 1963.1.12.1), which shows these features well, they even overlie the small male zooecia. In the younger portion of the specimen the zooecia are recumbent, with a series of distinct chambers (areolar? kenozooecial?) along the interzooecial grooves, and a superficial layer just beginning to form (Text-fig. 3, c.f. Osburn, 1933, pl. 9, figs. 1, 2). The zooecia in the older portion (Text-fig. 4) are in the jumbled, semi-erect condition, with asexual and both kinds of sexual zooecia present. As in the recumbent part, marginal chambers are very well developed, and the attachment of the basal surface of the younger zooecia to the frontal surface of the older ones is well seen. There is, moreover, in some places an appearance as if the zooecia and incipient zooecia were budded from the chambers (c.f. the relation of the zooecia of *R. doliaris* to the kenozooecia), but special study is required to ascertain whether this is so and what is the real nature of the chambers.

The difference in the form of the zoarium as a whole in *Hippothoa hyalina* and *Reginella doliaris* presumably depends on the fact that the primary growth of *H. hyalina* is an ordinary recumbent crust and only the secondarily developed individuals are superimposed on their neighbours ; whereas in *R. doliaris* it appears that the first formed zooecia (ancestrula not recognized) are erect and all the zooecia are budded in the one manner and applied to erect predecessors.

Generic position : *R. doliaris* resembles the type-species of *Reginella* in the characters of its frontal shield and flattened spines, and in having septula. *Cribrilina* Gray, type-species *C. punctata* (Hassall), has much in common with *Reginella* (see Osburn, 1950 : 174 (key) and 177), but possesses pore-chambers (dietellae).

Lumen-pores are not visible in the strongly calcified costae of *R. doliaris*, but they may be inconspicuous, and are sometimes not visible, in dry material of *R. furcata*, although they show well in transparent preparations of that species.

The erect position of the zooecia is probably not an important distinction between *R. doliaris* and typical *Reginella*, for the gradation from recumbent to erect zooecia is known in various genera, for example, *Beania* (see Hastings, 1943 : 408 (key), 413, c.f. *B. hirtissima* and *B. fragilis*).

Ovicells have not been seen in *R. doliaris*, and it differs from *R. furcata* in the conical form of the colony, and in the part played in its construction by heterozooecia (both kenozooecia and avicularia).

As already mentioned, avicularia are absent in the type-species of *Reginella*. Those of *R. doliaris* differ from those of *R.* (*Metracolposa*) *robusta* (see Canu & Bassler, 1917 : 35 ; 1920, pl. 40, fig. 2) in not having a complete cross-bar (pivot). In this feature *R. doliaris* resembles *Cribrilina*.

According to Jullien's description *Cribrilina alcicornis* Jullien (1883 : 508, pl. 14, figs. 23–25 ; Calvet 1907 : 399), a deep-water species from the Atlantic, off Spain, agrees with *R. furcata* in the characters of its frontal shield, and in having four flattened oral spines and a keeled hyperstomial ovicell.

In some respects *R. alcicornis* is intermediate between *R. doliaris* and more typical *Reginella* species. The " grandes ponctuations " in the interzooecial grooves appear to be kenozooecia comparable to those of *R. doliaris ;* and the avicularia are placed in the interzooecial grooves on each side of the orifice, and are without a cross-bar ; both points of resemblance to *R. doliaris*. The zoarium is, however, encrusting.

It is possible that the peculiarities of the colony of *R. doliaris* are of generic value, but it seems undesirable to introduce a new genus on the basis of a single colony without ovicells, especially as the zooecia suggest a close relationship to *Reginella*.[1]

Another possibility is that *R. doliaris* and *R. alcicornis* should both be separated from *Reginella* on account of their kenozooecia, since there is no evidence that these are present in typical species of *Reginella*. Structures which appear to be kenozooecia are widely distributed in the Cribrimorpha, and their taxonomic significance is uncertain. Waters (1923 : 559) mentioned " zooeciules ", " closed zooecia ", " blind zooecia " and " accessory cellules ", to which should probably be added " kenozooecia " (Canu, 1910 : 846–847), " interoecial tissue " (Lang, 1916 : 82), and " interzooecial tissue with chambers " (Waters, 1923 : 566–567). A few of these structures, although closed, have the cribriform wall, and are certainly equivalent to zooecia. In most, if not all, of the others their kenozooecial nature may be inferred. The part played by them in the building of the colony is various.

Membraniporella agassizii Smitt (1873 : 11, pl. 5, figs. 103–106) is a particularly interesting example. I have not seen a specimen of this deep-water species, which has not been rediscovered[2] (Osburn, 1940 : 404, and verbal communications from Dr. A. H. Cheetham and Dr. R. Lagaaij). However, Smitt gave a full description and excellent figures. The young zooecia have the characters of a typical *Membraniporella* except that they build an erect, branching, quadriserial colony. Gradually a profuse growth of kenozooecia and small avicularia envelopes these zooecia, appearing first in the interzooecial grooves, then spreading over the gymnocyst and finally covering the frontal shield. These older parts of the colony could be taken, superficially, for an ascophoran with a massive, thickened wall. (Have we here a hint (c.f. Smitt, p. 10) of how a pleurocyst may have evolved?) See Addendum.

In view of the evidence of a widespread tendency to the development of kenozooecia in various types of Cribrimorpha, I do not regard their development in *R. alcicornis* and *R. doliaris* as necessarily of generic importance. Conclusions drawn without seeing any specimen of the one species, and from a single specimen without ovicells of the other must be tentative, but, taking all the factors mentioned into consideration, I refer both species to *Reginella*.

[1]On a visit to this country in 1955 Professor D. A. Brown read the script of this paper, and told me that he had recently completed a paper in which he had independently referred *Cribrilina alcicornis* and *Cellepora doliaris* to *Reginella* (see Brown, 1958 : 53).

[2]This is probably because subsequent collecting has mostly been in shallower water. Dr. Lagaaij (*in litt.*) has pointed out that Smitt's material came from 450 fms., at one of his two deepest stations (see Pourtalès, 1871 : 3), and that the numerous samples of Polyzoa from the Gulf of Mexico and Straits of Florida which he himself has examined included few from deep-water and only one from below 400 fms.

5. COMPARISON OF *REGINELLA DOLIARIS* AND *CONESCHARELLINA*

The differences between *R. doliaris* and the Conescharellinidae are such as to place them in different major groups, but they show zoarial resemblances in which they appear to afford an interesting example of convergence.

R. doliaris resembles the Conescharellinidae in the orientation of its orifices, the hinge of the operculum being on the side towards the periphery of the colony. In the Conescharellinidae the orientation of the zooecium and the homologies of its walls are matters for deduction and discussion.[1] In *R. doliaris* they are settled beyond question by the clearly recognizable cribrimorph frontal walls, which show that the orifice is in the normal position in relation to the frontal wall. Further comparison of the two is thus of special interest.

R. doliaris resembles *Conescharellina* in its more or less conical colony, built, with a profusion of avicularia and kenozooecia, by means of budding of new zooecia in the angles between existing ones.

The resemblance between the genus *Conescharellina* and *R. doliaris* goes even further. Silén (p. 20) has described the row of pores along the lateral wall of the zooecium and the lateral budding of *Conescharellina*, *Flabellopora*[2] and *Crucescharellina*. These pores (which may perhaps be small pore-chambers) are comparable to the lateral kenozooecia of *R. doliaris* in their position in relation to the zooecia, to the colony as a whole, and to the distal avicularia ; and the buds appear to arise similarly, except that in *Conescharellina* there is usually a regularity in the budding sequence which produces a geometrically exact arrangement of zooecia not found in *R. doliaris*.

The photograph of *C. breviconica* (pl. 1, fig. 4) illustrates some of these points. For purposes of comparison I shall assume that the orientation of the zooecia is the same as in *R. doliaris*, and call the zooecial wall at the growing edge of the cone the " frontal wall ". The line of pores belonging to an incomplete zooecium can be seen to be applied to the frontal wall of an underlying zooecium and aligned with an avicularium at the convex surface of the colony, just as the line of kenozooecia in *R. doliaris* is applied to the frontal wall of a zooecium and aligned with a surface avicularium (pl. 3, fig. 1).

It thus seems possible that the budding of the Conescharellinidae (whether from one or both series of pores) may be closely comparable to that of *R. doliaris*, and their structure to be interpreted in the same way. Whether this is ultimately

[1]See particularly Silén (1947 : 18) and Harmer (1957 : 722). Bassler (1953 : G230) adopted Silén's interpretation. Earlier Canu & Bassler (1929 : 498) regarded the zooecia of *Conescharellina* and *Flabellopora* as being orientated in the same way as those of *Reginella doliaris* now prove to be, and stated (legend to text-fig. 208C) that the " anatomical arrangements are the same as in other Cheilostomes ". But, because the orifice is in a plane at an angle to that of the supposed frontal wall, they regarded it as on the distal wall. Such a difference in plane between the orifice and the rest of the frontal wall can, however, be seen in normally orientated erect zooecia of many other Polyzoa (e.g. various *Cellepora* spp.) and does not call for special interpretation.

[2]Harmer (1957 : 753) gave an interesting description of the very curious colony of *Flabellopora irregularis* Canu & Bassler, in which the orifices of alternate series of zooecia open on opposite surfaces of the colony. There is one point which may usefully be added to his account, namely, that the proximal ends of the zooecia are separated from the surface of the colony by the heterozooecia (probably kenozooecia as well as avicularia) which form the irregular crust surrounding the adjacent orifices, shown in Harmer's pl. 49, figs. 2, 4.

confirmed or not, *R. doliaris* is of interest and importance because it shows that it is possible for the apparently inverted arrangement to arise without the major changes in the proportions and relations of parts of the zooecia that have been postulated in attempts to interpret the Conescharellinid colony.

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8. ADDENDA

1. I have now examined Smitt's figured specimen of *Membraniporella agassizii*, see p. 258 above, and confirmed his account and figures. I am grateful to Dr. A. Andersson of the Riksmuseum, Stockholm, for lending the specimen.

2. Bobin & Prenant (1963, *Cah. Biol. mar.* 4: 40 *et. seq.*) have studied living ovicells of a species of *Bugula* with the calcareous parts shallow, see p. 250 above.